



## Population genetic evidence for a unique resource of Nile tilapia in Lake Tanganyika, East Africa

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1 **Population genetic evidence for a unique resource of Nile tilapia in**  
2 **Lake Tanganyika, East Africa**

3

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20

21 Nile tilapia (*Oreochromis niloticus*) is one of the most important species in Tanzania for inland  
22 fisheries and aquaculture. Although indigenous to the country, it is only naturally distributed  
23 within the margins of Lake Tanganyika and peripheral water bodies. The widespread  
24 distribution across other parts of the country is a consequence of introductions that started in  
25 the 1950s. We investigated the population genetic structure of Nile tilapia across Tanzania using  
26 nuclear microsatellite markers, and compared the head and body morphology of populations  
27 using geometric morphometric analyses. We found the Lake Tanganyika population to be  
28 genetically distinct from the introduced populations. However, there were no clear  
29 morphological differences in head and body shape that distinguished the Lake Tanganyika  
30 population from the others. We conclude that the Lake Tanganyika population of Nile tilapia  
31 represents a unique genetic resource within the country. We suggest that Nile tilapia aquaculture  
32 within the Lake Tanganyika catchment should be restricted to the indigenous strain.

33

34 **Keywords:** invasive species, hybridization, conservation genetics, stock structure.

## 35 **Introduction**

36

37 The ability of species to adapt to changing environmental conditions is dependent on the  
38 availability of standing genetic variation on which selection can act (Hoban et al. 2103). Both  
39 capture fisheries and aquaculture practices can deplete genetic diversity through the effects of  
40 size-selective harvesting (Frost et al. 2006; Pinsky & Palumbi 2013). Moreover, since many  
41 capture fisheries and aquaculture enterprises globally are based on species that have been  
42 introduced from other regions of the world, then such populations may particularly prone to  
43 founder events and episodes of strong selection associated with adaptation to new environments  
44 (Willoughby et al. 2018). Thus, the identification and conservation of natural genetic resources  
45 of species widely used in both aquaculture and capture fisheries could in the long-term help to  
46 mitigate against losses of genetic diversity and sustain fisheries production (Lind et al. 2012a).

47         Global production of Nile tilapia *Oreochromis niloticus* (L. 1758) within aquaculture  
48 and capture fisheries has been growing at an exponential rate since the 1990s (FAO 2018), and  
49 it is now one of the most widely cultured and fished species across tropical and subtropical  
50 freshwaters, including those of China, southeast Asia, north Africa, the Levant and central  
51 America (Deines et al. 2016). Moreover, since Nile tilapia is becoming a major aquaculture  
52 species in sub-Saharan Africa, the production of this species is likely be substantially increased  
53 as demand for farmed fish increases over the coming decades in line with human population  
54 growth.

55         Nile tilapia has a primary natural distribution in lakes and slow flowing rivers across  
56 the Nile and Niger basins of northern Africa (Trewavas 1983). Across its natural range it is  
57 extensively exploited in capture fisheries, and it has also been successfully introduced to natural  
58 water bodies and impoundments throughout much of tropical Africa. One of the earliest and  
59 most notable introductions of Nile tilapia was into Lake Victoria in the 1950s, initially as an

60 accidental ‘contaminant’ of stocks of *Coptodon zillii* (Gervais 1848), before deliberate  
61 introductions to boost fisheries production (Trewavas 1983). The species subsequently  
62 underwent a major population increase in Lake Victoria (Goudswaard et al. 2002), and now  
63 supports an important fishery with estimated landings of ~70,000 tonnes in 2010 (Kolding et  
64 al. 2014).

65         Several spatially separated distinct subspecies of Nile tilapia have been recognised in  
66 Africa based on morphological differences (Trewavas 1983), consistent with strong natural  
67 population genetic substructure within the range of this species (Agnès et al. 1997; Bezault et  
68 al. 2011). This natural spatial diversity has the potential to be compromised by interbreeding  
69 with introduced populations following escapes from aquaculture facilities, or following  
70 deliberate introductions aimed at improving capture fisheries. Already, some genetically and  
71 phenotypically distinct native populations of Nile tilapia are considered threatened because of  
72 hybridization with invading species, for example the blue spotted tilapia (*Oreochromis*  
73 *leucostictus*) (Ndiwa et al. 2014).

74         Nile tilapia from Lake Tanganyika is the most southerly population within the natural  
75 range of the species. The evidence that Nile tilapia is native to Lake Tanganyika comes from  
76 capture records that date as far back as 1906 (Trewavas 1983; Van Steenberge et al. 2011),  
77 before the first continuous aquaculture and fisheries improvement research activities in East  
78 Africa that took place during the mid-20<sup>th</sup> century (EAFFRO 1967). Lake Tanganyika is within  
79 Congo drainage, and thus is presently disconnected from other parts of the natural range of the  
80 species. Precisely how Nile tilapia arrived in Lake Tanganyika is unclear, but it is possible that  
81 it arrived naturally from Lake Kivu within the last 9,500-14,000 years, after volcanic activity  
82 blocked the northern connection of Lake Kivu to the Nile system, forming the Ruzizi river  
83 which flows into the northern Lake Tanganyika (Snoeks et al. 1997; Danley et al. 2012). In  
84 support of this scenario is evidence that Nile tilapia is native to Lake Kivu (Snoeks et al. 1997),

85 which has a history of faunal connectivity with Lake Tanganyika, for example through shared  
86 distributions of the migratory cyprinids *Raiamas moori* (Boulenger 1900) and *Labeobarbus*  
87 *altianalis* (Boulenger 1900) (Snoeks et al. 1997).

88         Although several studies have tested for genetic evidence of hybridization between  
89 invasive Nile tilapia and indigenous *Oreochromis* within East Africa (Nyingi et al. 2007; Ndiwa  
90 et al. 2014; Shechonge et al. 2018; Bradbeer et al. 2019), there have been few studies of  
91 population-genetic differentiation among Nile tilapia populations of the region (Agnèse et al.  
92 1997; Fuerst et al. 2000; Nyingi et al. 2009; Bezault et al. 2011), and none have considered  
93 variation among populations in Tanzania. Thus, here we test for population-level genetic  
94 differences among populations of Nile tilapia in Tanzania, focussing on comparisons between  
95 the indigenous Lake Tanganyika Nile tilapia and populations known to be introduced elsewhere  
96 in the country for aquaculture and fisheries improvement. We also test for morphological  
97 differences between the Lake Tanganyika population and the introduced populations.

98

## 99 **Methods**

100

### 101 **Sampling**

102

103 We collected samples of Nile tilapia from eight locations during 2015 and 2016, within the  
104 catchments of the Pangani River and Lakes Victoria, Eyasi and Tanganyika (Table 1; Fig. 1).  
105 Samples were collected from artisanal fishers or from experimental fishing using a seine net or  
106 gill net. Samples from fishers were already dead at the time of collection, while live fish  
107 collected from the nets were subjected to an overdose of clove oil (eugenol) anaesthetic on  
108 landing. Individual fish were pinned out with the head facing left, photographed from a standard  
109 orientation, and individually labelled. From each fish, we collected a tissue sample (fin clip)

110 preserved in absolute ethanol. Whole fish were then preserved in absolute ethanol, before  
111 transfer to 70% IMS for long term storage.

112

113 DNA extraction and microsatellite genotyping.

114

115 A piece of fin tissue approximately 3 x 3 mm was air dried, and the DNA was extracted using  
116 the Promega Wizard DNA extraction kit. Individual samples were then analysed to quantify  
117 variation at 17 microsatellite loci (Supplementary Information Table 1), sourced from Saju et  
118 al. (2010) and Liu et al. (2013). PCR was performed in a volume of 10 $\mu$ l, consisting of 1 $\mu$ l  
119 DNA (~5ng), 5 $\mu$ l Mastermix and 4 $\mu$ l primer mix (10mM). Each primer was labelled with one  
120 dye from the ABI DS-33 set (either 6-FAM, VIC, PET, NED). PCR amplifications were  
121 conducted within one of two multiplex PCR amplifications. PCR conditions for each multiplex  
122 consisting of one denaturation step of 15 minutes at 95°C, followed by 35 cycles of 30 seconds  
123 denaturation at 94°C, 90 seconds annealing at 57°C and 60 seconds extension at 72°C, followed  
124 by a final extension step of 30 minutes at 60°C. Samples were run on an ABI 3500 automated  
125 sequencer against a LIZ 500 size standard, and allele sizes for each locus were identified using  
126 GeneMapper 4.1 (Applied Biosystems, MA).

127

128 Molecular data analysis

129

130 Individual loci were checked for significant deviation from Hardy-Weinberg equilibrium using  
131 Arlequin 3.5 (Excoffier and Lischer 2010). In the 126 tests of deviation from Hardy Weinberg  
132 Equilibrium across the 17 loci, 23 were significant at  $P < 0.05$ , and in 21 of those cases observed  
133 heterozygosity was lower than expected heterozygosity. However, only one locus (OM-01)  
134 showed a consistent deviation from Hardy-Weinberg equilibrium across populations (a

135 heterozygote deficit), and data for this locus were excluded from further analysis. To compare  
136 genetic diversity among populations, we calculated a standardised allelic richness for each locus  
137 within in each population using rarefaction within HP-Rare, selecting the option for a sample  
138 of 10 “genes” (Kalinowski 2005). We tested for significant differences in rarefied allelic  
139 richness among populations we used a general linear model in R 3.6.0 (R Core Team 2019),  
140 followed by estimation of least square means and implementation of Tukey’s *post-hoc* tests  
141 using the R package lsmeans (Lenth 2016).

142 To quantify population genetic subdivision, we used  $F_{ST}$  calculated in Genepop 4.2.  
143 (Rousset 2008), alongside Exact tests based on 10,000 dememorisation steps, and 100 batches  
144 of 10,000 iterations. To ordinate genetic differences among individuals we used Principal  
145 Component Analysis (PCA) implemented in adegenet 2.1.1 (Jombart & Ahmed 2011) in R  
146 3.6.0. To estimate the probability of individual membership to  $K$  populations we used Structure  
147 2.3.4 (Pritchard et al. 2000), with the admixture model, no location priors, and 10 runs each  
148 with 100,000 burn-in steps and 100,000 recorded steps. The Structure output was then entered  
149 into Clumpak (Kopelman et al. 2015) to estimate the optimal number of populations present in  
150 the dataset using the Evanno method (Evanno et al. 2005). The probability of membership of  
151 individuals to those clusters was then graphically illustrated.

152

### 153 Morphological analyses

154

155 The left side of each specimen was photographed in a standard orientation, alongside a scale  
156 bar. Images were loaded into tpsDIG 2.26 (Rohlf 2015), using a file generated in tpsUtil 1.74  
157 (Rohlf 2015) and a total of 24 landmarks were placed on a calibrated image of each individual  
158 (Fig. 2). The resultant landmark coordinates were then aligned using a Procrustes analysis in  
159 MorphoJ 1.06 (Klingenberg 2011), and the generated Procrustes coordinates were used in a



160 pooled between-groups regression against centroid size, generating size-standardised residual  
161 Procrustes coordinates. These size-standardised Procrustes coordinates were then used within  
162 a Principal Components Analysis (PCA) to ordinate observed shape differences among  
163 individuals in MorphoJ 1.07a (Klingenberg et al. 2011) We tested the significance of shape  
164 differences between populations along the two primary axis of shape variation (PC1 and PC2)  
165 using a general linear model in R 3.6.0, followed by Tukey's *post-hoc* tests of pairwise  
166 differences between populations.

167

## 168 **Results**

169

### 170 Population genetic structure and genetic diversity

171

172 Overall, there were highly significant genetic differences among the eight populations (Global  
173  $F_{ST} = 0.249$ ; Exact test  $P < 0.001$ ). Between the population pairs,  $F_{ST}$  ranged from 0.016 to  
174 0.431 (Table 2), and all populations were significantly different (Exact tests,  $P < 0.001$ ).  
175 Principal Component Analysis (PCA) separated three clusters of individuals along PCA axes 1  
176 and 2. One cluster comprised the population from Lake Tanganyika, a second cluster comprised  
177 the population from Mwamapuli, and the third cluster comprised individuals sampled from  
178 other locations (Fig. 3). Within this third cluster, populations from the eastern Pangani system  
179 (Kerenge, Kumba, Pangani Falls) were tightly clustered, while the populations from the western  
180 Pangani system (Nyumba ya Mungu, Kivulini) were closely clustered with those from Lake  
181 Victoria (Fig. 3).

182 The optimum number of genetic clusters in the dataset, according the Structure analysis  
183 applying the Evanno method was  $K = 7$  (Fig. 4). The analysis indicated that the populations  
184 from Lake Tanganyika, Mwamapuli, Lake Kumba and Nyumba ya Mungu were largely distinct

185 from one another, and the other populations. Meanwhile, the populations from Lake Victoria  
186 and Kivulini were similar in allelic composition. The populations from Kerenge and Pangani  
187 Falls were similar, albeit heterogeneous, with some individuals sharing considerable allelic  
188 similarity with the Lake Victoria population (Fig. 4).

189 Rarefied allelic richness differed significantly among loci ( $F_{16,105} = 9.213$ ,  $P < 0.001$ ),  
190 and among populations ( $F_{7,105} = 7.561$ ,  $P < 0.001$ ; Table 1). In *post-hoc* comparisons, the  
191 Pangani Falls population had elevated diversity relative to those from Kivulini, Lake Kumba,  
192 Mwamipuli and Lake Tanganyika, while the Lake Kumba population had lower genetic  
193 diversity than Kerenge, Mwamipuli and Lake Tanganyika (Table 1; Supplementary Information  
194 Table 2).

195

196 Morphological differences among populations

197

198 Principal Component axis 1 captured variation in head and eye size, with individuals with  
199 positive PC1 scores possessing relative elongate snouts and larger eyes than individuals with  
200 negative scores. Principal Component axis 2 captured variation in body depth, with individuals  
201 with positive PC2 scores possessing shallower body depth than individuals with negative scores  
202 (Figure 5). Overall there was a highly significant differences among populations along these  
203 two axes of morphological variation ( $F_{7,126} = 9.599$ ,  $P < 0.001$ ). In *post-hoc* tests we found  
204 significant morphological differences in 11 of the 28 pairwise comparisons (Table 3). However,  
205 we found no clear evidence of morphological separation of the Lake Tanganyika population  
206 from the introduced populations sampled elsewhere in Tanzania. Instead, the Lake Tanganyika  
207 population overlapped in morphospace with most populations.

208

209

## 210 **Discussion**

211

212 Our results demonstrate that Nile tilapia collected around the margins of north-eastern Lake  
213 Tanganyika are genetically distinct from those sampled elsewhere in Tanzania, despite the lack  
214 of any clear diagnostic morphological differences. The apparent genetic uniqueness of this  
215 Tanganyika population is consistent with a long-period of separation from other populations  
216 sampled in Tanzania.

217 It seems unlikely that the samples we obtained are exclusively a result of recent  
218 colonisation of the sampled region by an invasive strain, but it is not unusual for fish to escape  
219 aquaculture facilities and introgress with wild stocks (Faust et al. 2018; Wringe et al. 2018),  
220 and this can have consequences for ecologically-important phenotypes of the wild populations  
221 (Bolstad et al. 2017). We cannot rule out the possibility that the Nile tilapia samples we  
222 collected from the Lake Tanganyika catchment are contaminated with recent escapes from  
223 aquaculture systems within the basin. For example, the Chitralada strain of Nile tilapia from  
224 Thailand has been reported in aquaculture within Burundi (<https://bit.ly/2JvI0N3>;  
225 <https://bit.ly/2EfAGB9>), and thus is potentially inside the Lake Tanganyika catchment.  
226 Contamination from genetically similar non-native stocks could explain the apparently high  
227 allelic similarity between two individuals from the Lake Tanganyika and those from Nyumba-  
228 ya-Mungu dam (Fig. 4). However, further sampling of Nile tilapia across its native and  
229 introduced range across Africa is required to test for introgression between indigenous and  
230 introduced strains.

231

232

233 Genetic structuring of introduced populations

234

235 It is commonplace to find population genetic structuring among naturally occurring populations  
236 of Nile tilapia (Table 4). Nevertheless, our finding of the substantial genetic structure among  
237 the non-native populations of Nile tilapia in Tanzania (average  $F_{ST} = 0.191$ , standard deviation  
238 0.092) is perhaps surprising given the relatively recent introductions of the species into the  
239 country. The most plausible explanation is that the high levels of genetic differentiation are  
240 driven by demographic processes that influence genetic diversity, including founder events  
241 and/or selection, perhaps associated with fisheries activity. In experimental conditions, Eguia  
242 et al. (2005) showed strong genetic divergence ( $F_{ST} = 0.130$ ) between a control and size-  
243 selected populations of Nile tilapia over as few as four generations. Spatial connectivity may  
244 also have affected genetic similarity of the populations from Lake Kumba, Kerenge and Pangani  
245 falls which are near one another and connected by flowing waterways. Finally, the timescale of  
246 divergence may have been influenced the extent of genetic divergence observed. For example,  
247 the populations from the Kivulini fishponds and Lake Victoria are genetically similar, which  
248 was expected given that Lake Victoria was cited as the original source of the fish we sampled  
249 from the newly constructed ponds by the owner at the time of sampling.

250

251 Another explanation for the presence of population genetic structure among our studied  
252 introduced populations is that they were seeded from multiple geographically distinct sources.  
253 Different Nile tilapia strains commonly used in aquaculture in Asia, for example, have clear  
254 genetic differences when studied using microsatellite loci (Sukmanomon et al. 2012; Table 4).  
255 Certainly, not all Nile tilapia in the country are from the same source, as shown by the recent  
256 arrival of the Chitralada strain at ponds in Dar es Salaam (Shechonge et al. 2019). A further  
257 explanation is that genetic differentiation is partially linked to hybridization with other

258 *Oreochromis* species. Relatively rare hybridization events between *O. niloticus* and native  
259 species are known from multiple locations relevant to our sampling, including satellite lakes of  
260 Lake Victoria [*O. esculentus* (Graham 1928); Angienda et al. 2011], the Pangani falls dam [*O.*  
261 *korogwe* (Lowe 1955); Bradbeer et al. 2019] and Nyumba ya Mungu [*O. jipe* (Lowe 1955);  
262 Bradbeer et al. 2019].

263

264 Aquaculture potential and the conservation of an indigenous genetic resource

265

266 Increased aquaculture production is required to meet demands for fish protein from the growing  
267 human population (FAO, 2018). At present, the aquaculture production potential of the Lake  
268 Tanganyika Nile tilapia population is unknown. We are unaware of any aquaculture facilities  
269 using this strain, and typically aquaculture in the Tanzanian sector of the Lake Tanganyika  
270 catchment focusses primarily on the other large-bodied indigenous species *Oreochromis*  
271 *tanganicae* (Günther 1894) and *Oreochromis malagarasi* Trewavas 1983. Controlled growth  
272 trials of these two species, alongside indigenous Nile tilapia, would inform us of their collective  
273 aquaculture potential as the industry expands to support the growing human population of the  
274 region.

275

276 An expanding aquaculture industry requires strains of farmed fish that are resistant to emerging  
277 diseases and are able to thrive given the specific environmental conditions. The increasing  
278 importance of Nile tilapia in global aquaculture implies that genetic resources will be required  
279 to facilitate the selective breeding of improved varieties (Eknath and Hulata 2009; Lind et al.  
280 2012b). Our results indicating unique status of the Lake Tanganyika population imply that it  
281 should be valued for its potential to contribute to future selective breeding programmes. The  
282 introduction of Nile tilapia from other sources into the catchment could potentially lead to

283 intraspecific hybridization and the dilution or loss of this unique genetic resource. Already at  
284 least one potentially invasive populations of Nile tilapia of uncertain provenance is present in  
285 the upper Malagarasi river connected to Lake Tanganyika (Shechonge et al. 2019). Given the  
286 uncertainty regarding the outcome of direct contact between non-native and native strains of  
287 Nile tilapia, we suggest that further development of Nile tilapia aquaculture and fisheries in the  
288 region should be based on the indigenous population to reduce the likelihood of erosion of the  
289 Lake Tanganyika Nile tilapia genetic resource.

290

### 291 **Concluding remarks**

292

293 Key questions remaining from this study relate to the processes that have driven the patterns of  
294 spatial genetic variation in Tanzania, and to answer these requires more extensive sampling of  
295 both Nile tilapia and native *Oreochromis* populations in Tanzania. It also requires sampling of  
296 wild stocks in neighbouring countries, as well as the high-performance commercially farmed  
297 strains from which introduced broodstock could have been sourced. With the recent availability  
298 of high-quality reference genomes of Nile tilapia (Brawand et al. 2014; Conte et al. 2017), it is  
299 now possible to accurately conduct genome-wide analyses to quantify intraspecific gene flow,  
300 introgression and reconstruct population demography, and to map traits beneficial for fisheries  
301 production on the genome. Such information will further clarify the value of the Lake  
302 Tanganyika Nile tilapia population as a genetic resource, while potentially verifying and  
303 explaining the patterns of population genetic structuring we have recovered in this study.  
304 Knowledge of the genomic composition of populations in a comparative framework would also  
305 inform future investigations of phenotypic traits that could be useful for aquaculture and capture  
306 fisheries development, and potentially inform the development of future strains of this globally  
307 important species.

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314

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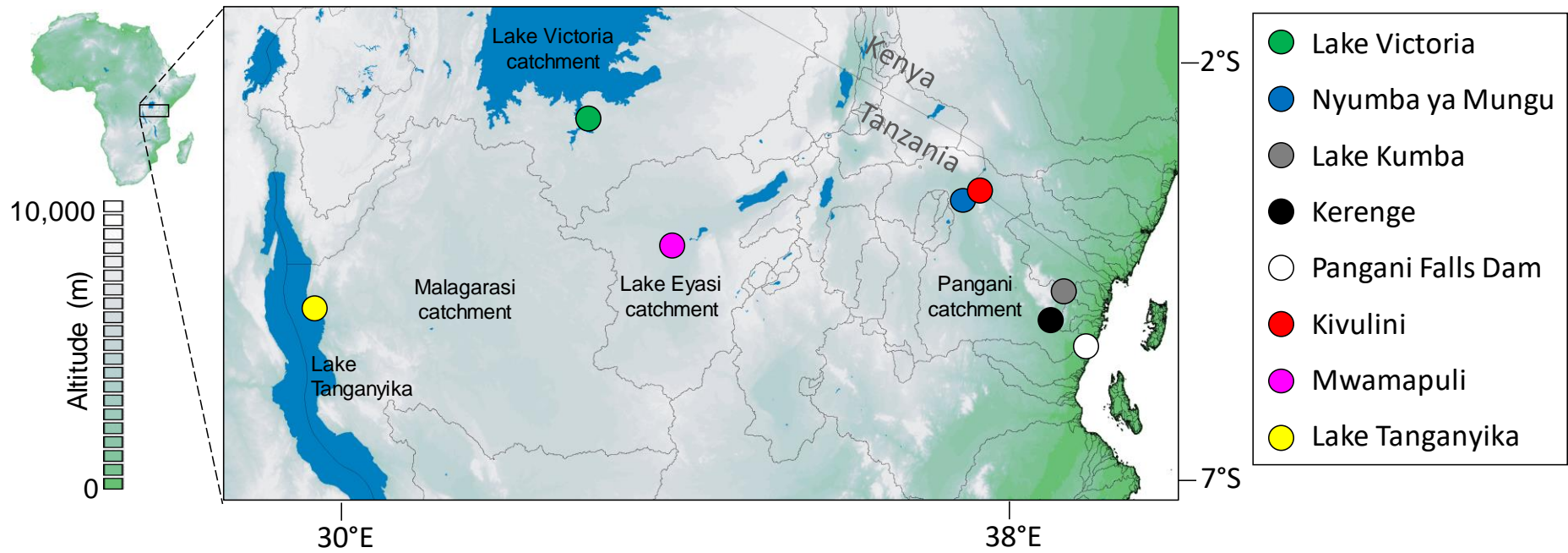
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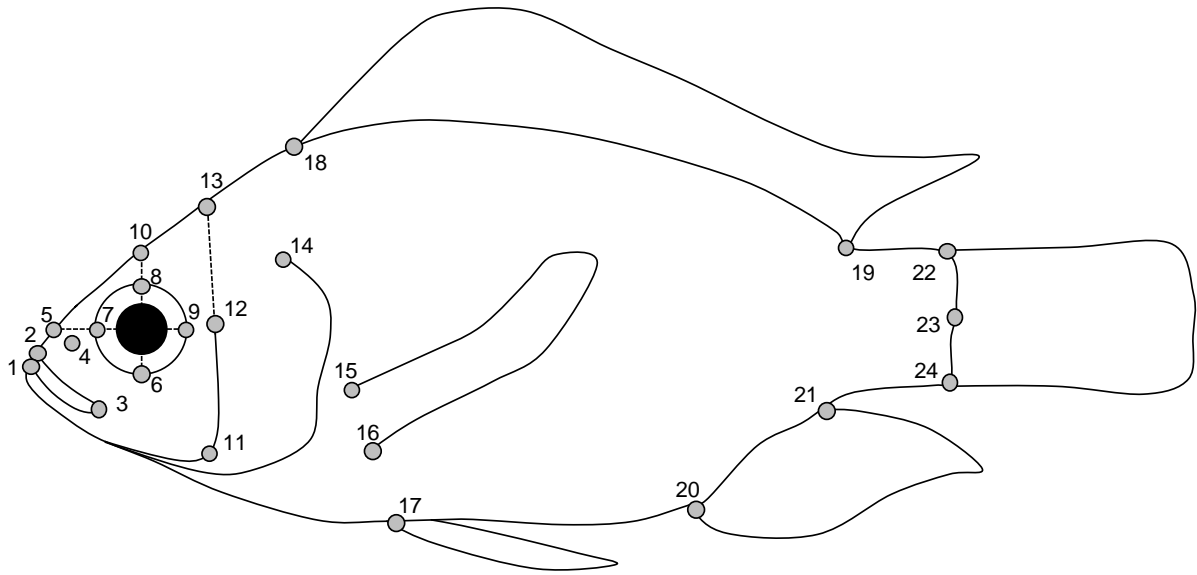
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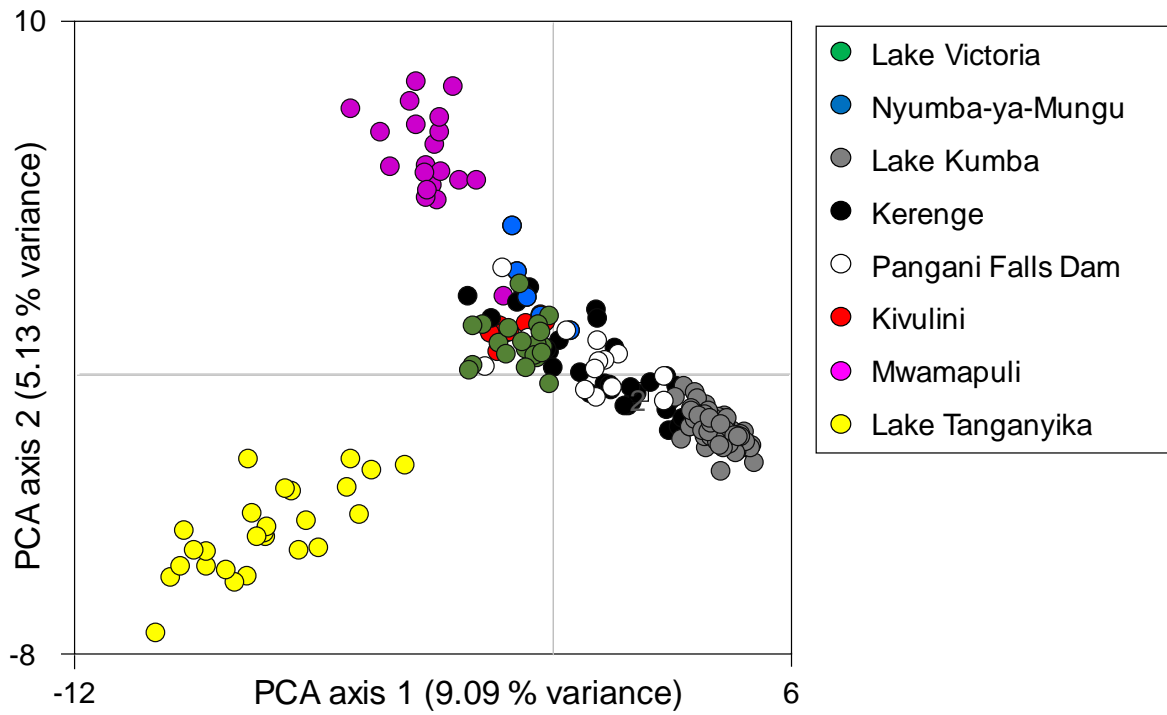
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459 **Fig. 1** Locations of eight sampling sites in northern Tanzania



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461 **Fig. 2** Landmarks used in geometric morphometric analysis of Nile tilapia.

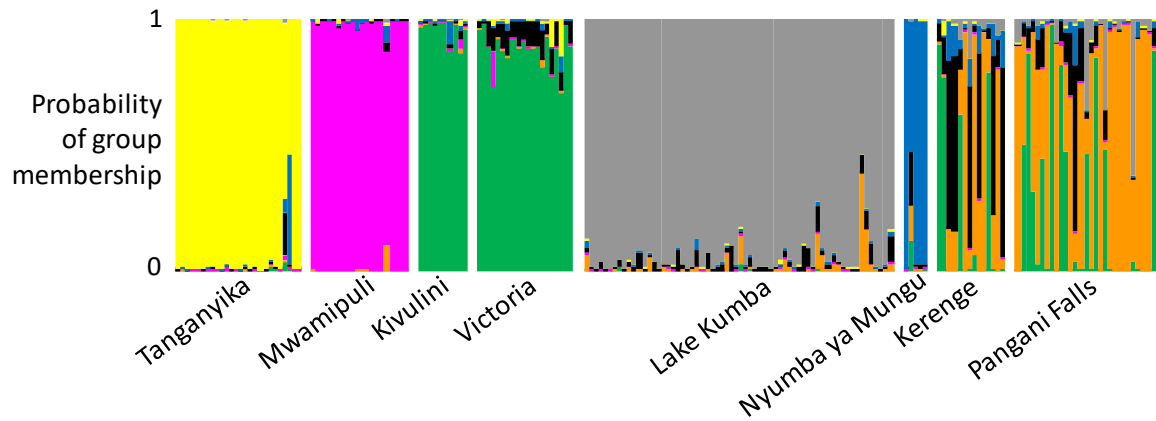


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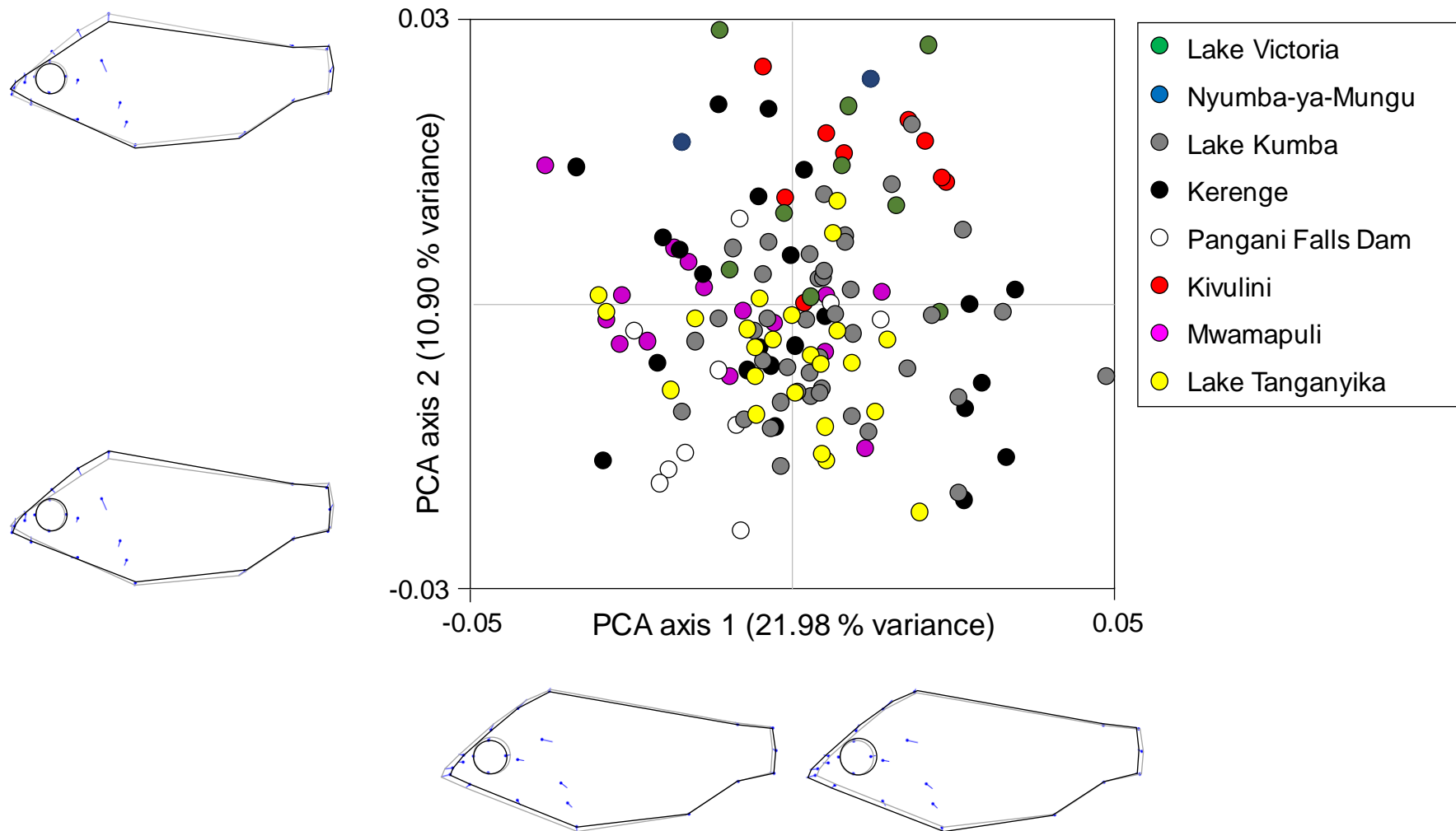
464 **Fig. 3** Principal Component ordination plot illustrating genetic differences among  
 465 individuals.





466

467 **Fig. 4** Structure plot of probability of that individuals belong to genetic groupings. The  
 468 optimal number of groups shown is  $K=7$ , following the Evanno method. Each colour  
 469 represents one genetic grouping.



470

471 **Fig. 5** Principal Component ordination plot illustrating shape variation among *O. niloticus* populations. Shape variation is illustrated using

472 outlined lollipop plots, with darker lines indicative of phenotypes at the extremes of each axis.

473 **Table 1.** Sampling localities and sample sizes for molecular and morphological analyses. RAR = Rarefied allelic richness (measured across 10  
 474 “genes”) in HPRare (Kalinowski 2005).

Site name	Coordinates	Sampling dates	Sampling method	N genetics	N morphology	RAR ( $\pm$ 95% CI)
Lake Tanganyika*	4.859 °S, 29.621°E 4.907°S, 29.665°E 5 211°S, 29.842°E	27-29 / 07 / 2016	Artisanal fishers	26	24	3.27 (0.39)
Mwamapuli	4.356°S, 33.876°E	02 / 08 / 2016	Seine net	20	15	3.22 (0.39)
Kivulini	3.479°S, 37.589°E	14 / 08 / 2015	Seine net	10	9	2.98 (0.37)
Kerenge	5.032°S, 38.548°E	12 / 08 / 2015	Seine net	30	23	3.65 (0.37)
Lake Kumba	4.806°S, 38.621°E	12 / 08 / 2015	Artisanal fishers	64	42	2.32 (0.37)
Nyumba ya Mungu	3.612°S, 37.459°E	14 / 08 / 2015	Artisanal fishers	5	2	3.42 (0.39)
Pangani falls	5.347°S, 38.645°E	19 / 08 / 2015	Gill net	14	10	4.14 (0.37)
Lake Victoria**	2.627°S, 32.899°E 2.588°S, 32.855°E	04-06 / 08 / 2016	Artisanal fishers	20	9	3.14 (0.43)

475 \*samples from 3 sites, n for genetics: Ujiji n = 4; Malagarasi n=2; Kigoma n=20. Samples were pooled for analyses as there was no evidence of significant genetic  
 476 structuring among them (Global  $F_{ST}$  = -0.011; Exact test  $P$  = 0.575).

477 \*\* samples from 2 sites, n for genetics: Lake Malimbe n = 14, Mwanza Gulf n = 6. Samples were pooled for analyses as there was no evidence of significant  
 478 genetic structuring among them (Global  $F_{ST}$  = -0.008; Exact test  $P$  = 0.215).

479 **Table 2.** Genetic differences among populations ( $F_{ST}$ ). All comparisons were highly  
 480 significantly different ( $P < 0.001$ ) in pairwise exact tests.

Population	Lake Tanganyika	Mwamapuli Kivulini	Kerenge	Lake Kumba	Nyumba ya Mungu	Pangani Falls
Mwamapuli	0.254					
Kivulini	0.284	0.228				
Kerenge	0.267	0.182	0.123			
Lake Kumba	0.431	0.325	0.344	0.149		
Nyumba ya Mungu	0.320	0.235	0.239	0.145	0.347	
Pangani Falls	0.253	0.171	0.122	0.016	0.158	0.088
Lake Victoria	0.269	0.212	0.087	0.130	0.340	0.237
						0.133

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484 **Table 3.** Results of *post-hoc* Tukey's tests (p-values) indicating significance of  
 485 morphological differences among populations, as captured along the first two axes of  
 486 morphological variation (PC1 and PC2; Figure 5).

Population	Lake Tanganyika	Mwamapuli Kivulini	Kerenge	Lake Kumba	Nyumba ya Mungu	Pangani Falls
Mwamapuli	0.957					
Kivulini	< 0.001	< 0.001				
Kerenge	0.834	0.272	0.002			
Lake Kumba	0.249	0.032	0.005	0.995		
Nyumba ya Mungu	0.426	0.196	0.999	0.798	0.906	
Pangani Falls	0.465	0.975	< 0.001	0.043	0.004	0.067
Lake Victoria	0.002	0.000	0.991	0.055	0.122	1.000
						< 0.001

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489 **Table 4.**  $F_{ST}$  values reported from published population genetic studies of Nile tilapia using microsatellite markers.

490

Studied populations	Number of microsatellite markers	Location	Number of comparisons (strains or populations)	Mean $F_{ST}$	Standard deviation of $F_{ST}$	Maximum $F_{ST}$	Minimum $F_{ST}$	Reference
Native range	9	Africa	10	0.340	0.177	0.723	0.054	Bezault et al. (2011)
Native range	6	Egypt	5	0.035	-	-	-	Hassanien & Gilbey (2005)
Native range	6	Kenya	4	0.216	0.050	0.290	0.127	Nyingi et al. (2009)
Native range	16	Kenya	6	0.164	0.099	0.352	0.018	Ndiwa et al. (2014)
Introduced range (feral)	8	Kenya	4	0.042	0.018	0.069	0.020	Angienda et al. (2010)
Introduced range (feral)	10	China	5	0.207	0.150	0.376	0.030	Gu et al. (2014)
Within culture (non feral)	14	Thailand	7	0.087	0.087	0.194	0.012	Sukmanomon et al. (2012)
Within culture (non feral)	14	Global	4	0.176	0.093	0.333	0.084	Rutten et al. (2004)

491

**Supplementary Information Table 1** Genetic diversity of 17 microsatellite loci at the sampling locations. N = sample size, HO = Observed heterozygosity, HE = Expected heterozygosity, P = probability of Hardy-Weinberg equilibrium.

Population	Locus	OM-01	OM-03	OM-04	OM-09	OMO043	OMO100	OMO248	OMO093	OMO114	OMO129	OMO161	OMO219	OMO229	OMO337	OMO391	OMO392	OMO397
Lake Tanganyika	N	23	26	-	26	26	26	24	19	24	25	17	19	25	25	22	16	25
	N alleles	13	6	-	8	4	6	3	3	6	4	5	4	4	3	4	4	7
	HO	0.478	0.615	-	0.615	0.462	0.692	0.500	0.368	0.792	0.600	0.529	0.316	0.640	0.120	0.273	0.750	0.640
	HE	0.848	0.673	-	0.809	0.482	0.732	0.401	0.681	0.650	0.541	0.683	0.286	0.644	0.256	0.253	0.554	0.788
	P	< 0.001	0.073	-	0.202	0.873	0.743	0.725	0.004	0.451	0.180	0.009	1.000	0.587	0.015	1.000	0.345	0.069
Mwamapuli	N	20	20	-	20	20	20	18	20	20	19	19	20	-	19	19	20	
	N alleles	8	5	-	8	5	4	5	3	4	3	2	6	5	-	4	3	4
	HO	0.550	0.500	-	0.650	0.550	0.700	0.650	0.500	0.700	0.500	0.263	0.842	0.650	-	0.632	0.316	0.300
	HE	0.788	0.729	-	0.794	0.553	0.694	0.685	0.624	0.724	0.627	0.422	0.770	0.719	-	0.636	0.522	0.350
	P	0.034	0.076	-	0.112	0.478	0.607	0.706	0.182	0.397	0.103	0.125	0.836	0.095	-	0.926	0.098	0.575
Kivulini	N	9	9	9	9	9	9	9	10	10	10	10	10	10	-	10	10	10
	N alleles	5	5	2	4	3	6	4	2	4	4	3	2	4	-	3	4	6
	HO	0.333	0.778	0.111	0.778	0.444	1.000	0.556	0.800	0.900	0.800	0.600	0.300	0.600	-	0.200	0.500	0.900
	HE	0.778	0.680	0.111	0.575	0.451	0.837	0.471	0.505	0.684	0.595	0.584	0.395	0.489	-	0.195	0.489	0.832
	P	0.005	0.117	1.000	0.762	0.250	0.628	1.000	0.173	0.545	0.581	0.449	0.480	1.000	-	1.000	0.446	0.321
Kerenge	N	28	30	28	30	30	30	30	30	30	30	30	30	30	30	30	30	30
	N alleles	12	10	4	8	5	7	3	3	6	6	3	3	7	2	6	4	7
	HO	0.643	0.700	0.179	0.767	0.367	0.767	0.667	0.633	0.867	0.533	0.633	0.567	0.667	0.267	0.800	0.500	0.567
	HE	0.904	0.764	0.424	0.602	0.328	0.762	0.621	0.671	0.781	0.686	0.660	0.635	0.676	0.325	0.773	0.580	0.802
	P	0.001	0.772	< 0.001	0.967	1.000	0.055	0.177	1.000	0.369	0.010	0.103	0.534	0.897	0.305	0.040	0.346	0.028

**Supplementary Information Table 1** continued

Population	Locus	OM-01	OM-03	OM-04	OM-09	OMO043	OMO100	OMO248	OMO093	OMO114	OMO129	OMO161	OMO219	OMO229	OMO337	OMO391	OMO392	OMO397
Lake Kumba	N	62	63	64	63	63	63	63	60	64	64	62	57	64	64	64	61	64
	N alleles	5	4	3	5	2	5	4	3	4	3	2	4	4	2	4	3	5
	HO	0.500	0.714	0.047	0.921	0.016	0.206	0.397	0.583	0.609	0.297	0.532	0.544	0.281	0.281	0.531	0.541	0.563
	HE	0.544	0.682	0.046	0.592	0.016	0.230	0.427	0.618	0.561	0.374	0.504	0.499	0.315	0.496	0.589	0.505	0.622
	P	0.020	0.848	1.000	< 0.001	1.000	0.162	0.763	0.116	0.586	0.136	0.799	0.708	0.002	0.001	0.712	0.852	0.427
Nyumba-ya-Mungu	N	3	5	4	5	5	5	5	-	5	5	5	5	5	-	5	5	5
	N alleles	4	4	2	4	4	3	5	-	3	3	3	3	5	-	4	3	6
	HO	0.333	0.600	0.500	1.000	0.400	0.600	0.800	-	1.000	0.600	0.800	0.000	1.000	-	1.000	0.400	0.800
	HE	0.867	0.778	0.429	0.711	0.778	0.644	0.756	-	0.644	0.511	0.644	0.622	0.844	-	0.733	0.733	0.778
	P	0.067	0.693	1.000	0.428	0.048	1.000	0.487	-	0.173	1.000	0.619	0.016	0.846	-	0.387	0.544	0.872
Pangani Falls	N	14	13	9	14	14	14	14	14	14	13	14	14	14	14	14	14	14
	N alleles	10	6	6	6	5	4	4	3	6	7	4	4	8	2	5	5	7
	HO	0.429	0.692	0.444	0.929	0.429	0.500	0.429	0.500	0.571	0.769	0.571	0.500	0.786	0.214	0.643	0.643	0.714
	HE	0.902	0.806	0.719	0.688	0.479	0.730	0.611	0.574	0.828	0.855	0.696	0.696	0.849	0.389	0.746	0.675	0.870
	P	< 0.001	0.207	0.023	0.651	0.221	0.030	0.276	0.533	0.048	0.052	0.830	0.421	0.187	0.142	0.350	0.810	0.230
Lake Victoria	N	18	19	10	18	6	-	20	-	19	18	-	20	20	-	20	19	20
	N alleles	11	8	2	8	3	-	4	-	4	3	-	4	5	-	2	3	6
	HO	0.556	0.789	0.000	0.500	0.500	-	0.250	-	0.684	0.444	-	0.500	0.750	-	0.200	0.632	0.650
	HE	0.867	0.815	0.189	0.784	0.621	-	0.233	-	0.698	0.532	-	0.596	0.626	-	0.185	0.496	0.673
	P	0.001	0.321	0.053	0.003	0.655	-	1.000	-	0.419	0.786	-	0.568	0.968	-	1.000	0.421	0.330

**Supplementary Information Table 2** *Post-hoc* tests of differences in genetic diversity

(Rarefied Allelic Richness) among populations.

<b>Population pair</b>	<b>P</b>
Kerenge - Kivulini	0.2222
Kerenge – Kumba	0.0001
Kerenge – Mwamipuli	0.7768
Kerenge – Nyumba ya Mungu	0.9916
Kerenge – Pangani falls	0.5909
Kerenge – Lake Tanganyika	0.8648
Kerenge – Lake Victoria	0.6729
Kivulini – Kumba	0.2296
Kivulini – Mwamipuli	0.9882
Kivulini - Nyumba ya Mungu	0.7478
Kivulini – Pangani falls	0.0009
Kivulini – Lake Tanganyika	0.9667
Kivulini – Lake Victoria	0.9993
Kumba – Mwamipuli	0.0301
Kumba - Nyumba ya Mungu	0.0028
Kumba – Pangani falls	< 0.0001
Kumba – Lake Tanganyika	0.01790
Kumba – Lake Victoria	0.1039
Mwamipuli - Nyumba ya Mungu	0.9962
Mwamipuli – Pangani falls	0.0229
Mwamipuli – Laek Tanganyika	1.0000
Mwamipuli – Lake Victoria	1.0000
Nyumba ya Mungu – Pangani falls	0.1560
Nyumba ya Mungu – Lake Tanganyika	0.9993
Nyumba ya Mungu – Lake Victoria	0.9816
Pangani falls – Lake Tanganyika	0.0380
Pangani falls– Lake Victoria	0.0192
Lake Tanganyika – Lake Victoria	0.9999